

THE OCCURRENCE, DISTRIBUTION AND ATTACHMENT OF THE
PEDUNCULATE BARNACLE *OCTOLASMIS MÜLLERI* (COKER)
ON THE GILLS OF CRABS, PARTICULARLY THE BLUE
CRAB, *CALLINECTES SAPIDUS* RATHBUN¹

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During the summer of 1973 crabs were collected regularly from Beaufort Inlet, North Carolina and examined for the presence of the epizoid barnacle, *Octolasmis mülleri* (Coker), within the branchial chambers. The blue crab, *Callinectes sapidus* Rathbun is the most common crab in Beaufort Inlet (Dudley and Judy, 1971) and was therefore chosen as the host for a detailed study of *O. mülleri*. The life-history and migrations of *C. sapidus* (Van Engel, 1958; Cargo, 1958; Costlow and Bookhout, 1959; Tagatz, 1968; Judy and Dudley, 1970; Dudley and Judy, 1971) have been studied because this crab is exploited commercially. The migrations of this crab may also influence the life-histories of epizoids. The present study investigates the occurrence, distribution and mode of attachment of the epizoid *O. mülleri* on the gills of *C. sapidus* and discusses the possible correlations with the life cycle and habits of the crab.

MATERIALS AND METHODS

When barnacles were found to be present in a blue crab, all the gills were removed and the number and position of the barnacles on each gill noted.

During July several blue crabs were collected which had only the recently settled cypris larva of the barnacle present on the gills. These larvae, together with the portion of the gill to which they were attached, were fixed for a histological study. Adult specimens of *O. mülleri* were also fixed in Carnoy's and Bouin's fixatives for a histological study of the cement apparatus. Wax sections (5 μ thick) were stained with Heidenhain's azan. The peduncles of both *O. mülleri* and the related *Lepas anatifera* were fixed in 1% OsO₄ in veronal buffer, dehydrated and embedded in Araldite. One μ thick transverse sections of the peduncles stained with toluidine blue in borax (1% aqueous solution) were examined with the light microscope.

RESULTS

The 4th gill of *C. sapidus* is drawn diagrammatically in Figure 1a. It is composed of many paired platelets (pl.) which have well defined spines and knobs around their outer margin (Fig. 1b). The larger efferent blood vessel (e.v.) and the smaller afferent vessel (a.v.) are situated on the inner and outer side of the

¹ This study was carried out at the Duke Marine Laboratory, Beaufort, N.C. 28516.

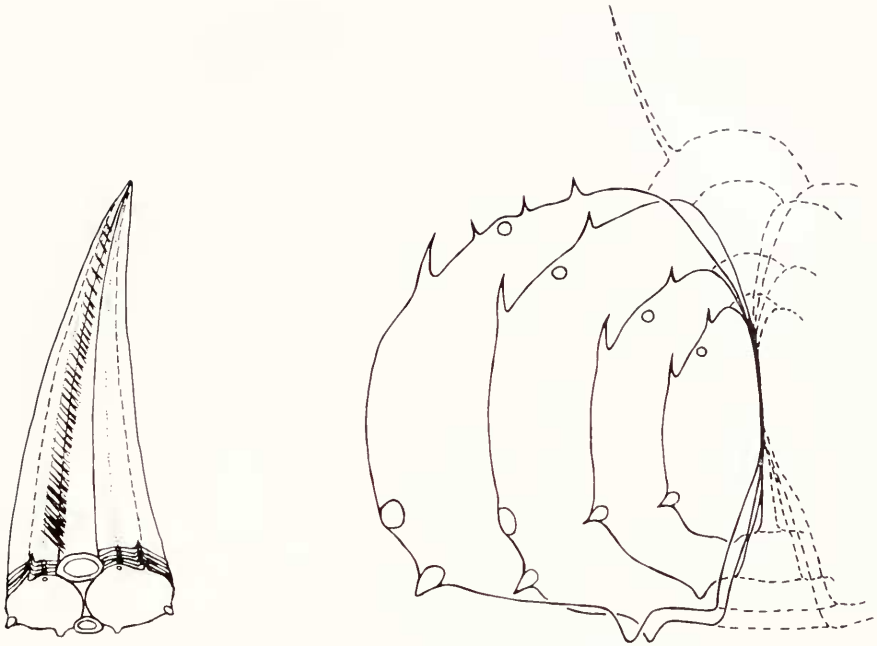


FIGURE 1. (a) A drawing of the 4th gill of *Callinectes sapidus* showing the paired platelets (pl.), small afferent vessel (a.v.) and larger efferent vessel (e.v.); (b) drawings of gill platelets taken from different regions (1, 2, 3, 4) of the same gill. The platelets are divided into afferent (aff.) and efferent (eff.) zones and show the marginal projections: spines a, b, d, g and knobs c and e; a.v., afferent vessel; e.v., efferent vessel; sp., spine.

gill respectively. Most of the marginal projections of the platelets emerge at an angle to the surface of the platelet itself and some of these presumably act as "spacers" keeping the platelets separated and allowing water circulation. The spines a, b, d, f and g (Fig. 1b) can be picked out with the naked eye, but the more interior knobs c and e are hidden from view. In the proximal region of a gill the platelets possess all the spines and knobs previously mentioned, but spines g and knob c disappear towards the distal end. Seven of the eight pairs of gills in the crab lie close to one another so that platelets of adjacent gills touch. Each platelet can be divided equally into afferent and efferent zones (Fig. 1b). Examina-

TABLE I

Variation in the barnacles settled on each of 8 pairs of gills from 25 blue crabs.

Source of variation	Degrees of freedom	Mean square	F-ratio
Between gills	7	0.1961	147
Within gills	192	0.00133	
Total	199		

tion of 400 gills (25 blue crabs) revealed that 83.06% of the barnacle population occurred on the efferent side and 16.94% on the afferent side. The barnacle population on the efferent side of the gills was analysed in more detail. The mean number of *O. mülleri* $n_1, n_2 \dots n_8$ was assessed on each of the eight pairs of gills of 25 crabs and the proportion

$$P_x = \frac{n_x}{\sum_{x=1}^8 n_x}$$

calculated for each gill pair. Analyses of variances was carried out on the ratios $p_1 \dots p_8$ for the 25 crabs. The results presented in Table I show that the variation between the mean proportionate infestation rate on the eight different pairs of gills exceeded significantly the variation between replicates ($F = 147, P < 0.001$). It

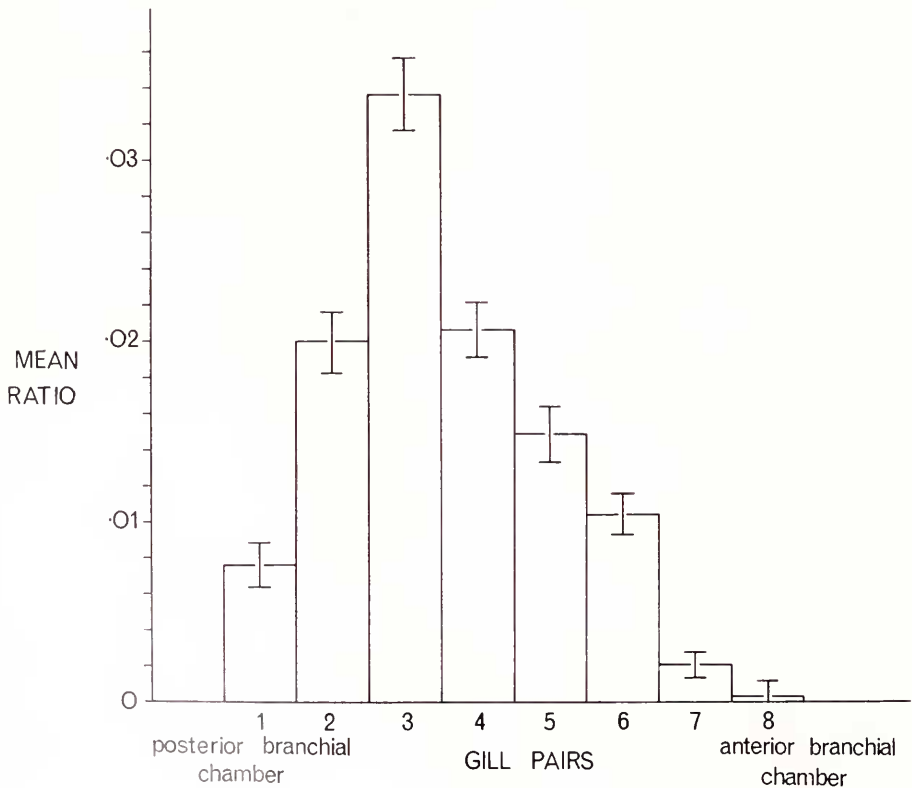


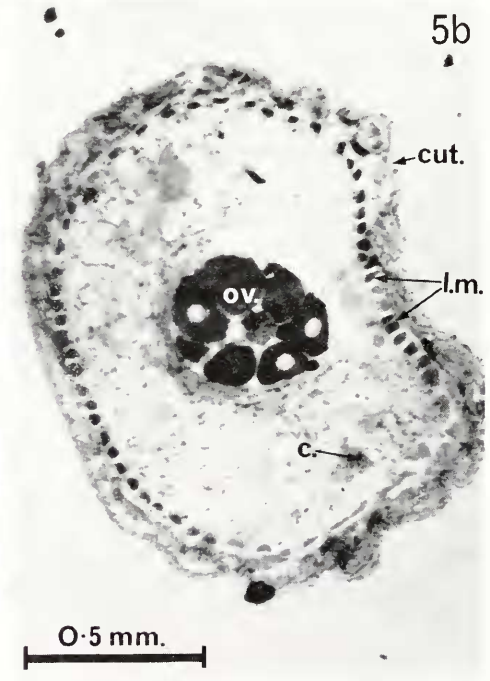
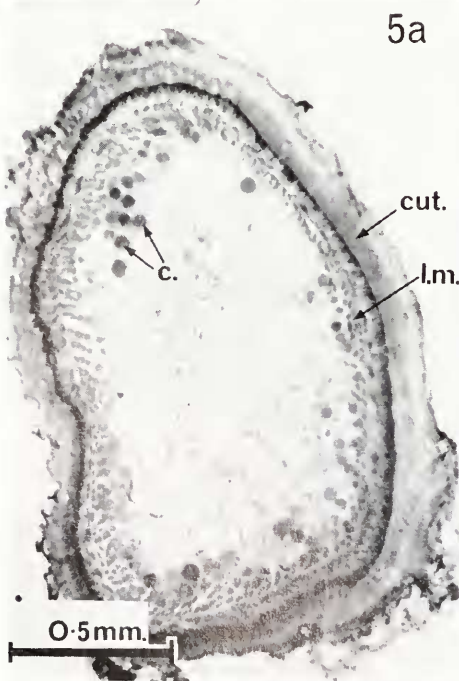
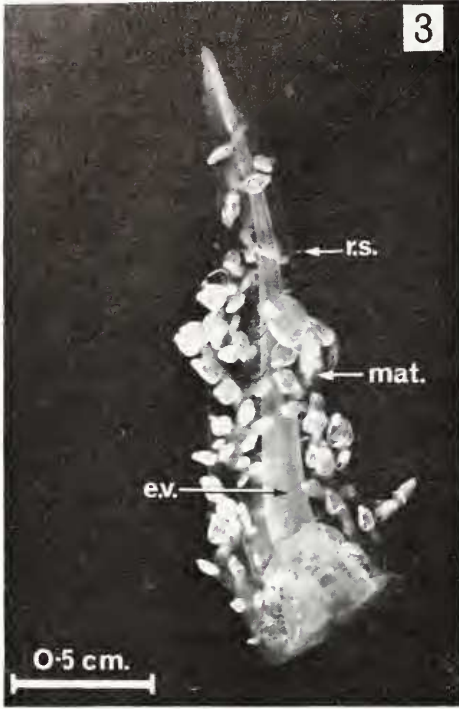
FIGURE 2. Histogram showing the mean ratios $\left[\frac{\text{No. of barnacles on gill pair}}{\text{Total No. barnacles on crab}} \right]$ of barnacles on the different gills of *C. sapidus*. The vertical bars indicate the fiducial limits at the 95% level of significance.

TABLE II
List of crabs on which Octolasmis mülleri has been found.

Crab	Reference	Habitat (from Williams, 1965)
* <i>Arenaeus cribrarius</i> Lamarck		Ocean. Close to shore. Seldom enters estuaries. Shore—37 fathoms.
<i>Calappa flammea</i> Herbst	Humes, 1941.	Ocean. Surface—40 fathoms.
<i>Callinectes ornatus</i> Ordway	DeTurk, 1940; Humes, 1941.	Coastal. Often estuaries, sometimes to fresh water. Surface—40 fathoms.
* <i>Callinectes sapidus</i> Rathbun	Coker, 1902; Pilsbry, 1907; Scarff, 1966; Scrocco & Fabianek, 1969.	Shallow ocean. Estuaries to fresh water. Surface— 20 fathoms.
* <i>Hepatus epheliticus</i> L.	DeTurk, 1940; Humes, 1941.	Ocean, Sometimes estuaries. 2–25 fathoms.
<i>Libinia dubia</i> H. Milne Edwards	DeTurk, 1940.	Ocean. Shore—25 fathoms.
* <i>Libinia emarginata</i> Leach	DeTurk, 1940; Coker, 1902.	Ocean. Shore—27 fathoms, occasionally 68 fathoms.
* <i>Menippe mercenaria</i> Say	Coker, 1902; Humes, 1941; Pearse, 1947.	Ocean and estuary. Surface— 28 fathoms.
* <i>Ovalipes ocellatus</i> Herbst		Ocean, close to shore. Surface—18 fathoms.
<i>Panopeus herbstii</i> H. Milne Edwards	Humes, 1941	Coastal. Often estuaries. Surface—12 fathoms.
* <i>Persephona punctata</i> <i>aquilonaris</i> Rathbun		Ocean. 2–30 fathoms.
* <i>Portunus spinimanus</i> Latreille	DeTurk, 1940.	Ocean. Surface—50 fathoms.
<i>Uca minax</i> Le Conte	Pearse, 1936.	Marshes. Some distance from high salinity water.

* Crabs examined in the present study.

should be noted that the procedure adopted eliminated the influence of differences in individual infestation rate between crabs. Comparison between the mean ratios of the barnacles on the gills is shown graphically in Figure 2. It can be seen that the largest number of barnacles is found attached to gill 3, the numbers decreasing progressively on either side of gill 3.



The efferent zone was split up into several regions (Fig. 1b) and the number of barnacles in these regions counted. Out of a total of 2,953 barnacles counted 1270 (43%) were found in the region between knob e and the efferent vessel, 701 (24%) were associated with spine d, 497 (17%) were associated with knob e, 344 (12%) were found in the region between knob e and spine d and 141 (5%) on the efferent vessel itself.

Cyprids enter the branchial chamber in the inhalant respiratory current of the blue crab. They pass into the hypobranchial side of the branchial chamber. Since the gills are closely opposed to one another the cyprids are unable to pass through to the hyperbranchial side; the gills are therefore a filter to the cyprids. The cyprids must be able to adhere temporarily to the gills whilst searching for a suitable site of attachment, for periodically the respiratory current is reversed by the crab. *O. mülleri* not only settles on a wide variety of crabs (see Table II), but also on different sized crabs within each species (different age groups). In all juvenile crabs moulting is frequent and barnacles which have settled will be shed with the exuvia before reaching maturity; once outside of the host *O. mülleri* is thought to perish. The successful life cycle of *O. mülleri* therefore takes place either in crabs which will no longer moult *i.e.* mated female blue crabs, or on mature crabs which although able to moult still go through prolonged intermoult periods. A large barnacle population on any one crab is composed of individuals ranging from recently settled larvae through to mature adults, Figure 3, showing that the barnacle has a long settling season in comparison with its life span between metamorphosis and maturity.

In addition to withstanding reversal of the respiratory current the cyprids must also survive the cleaning action of the epipodites of the second and third maxillipeds (see Pyle and Cronin, 1950). These epipodites have a fringing mass of setae which have back-curved hooks close to their tips (Fig. 4). The effectiveness of these cleaning appendages on exposed surfaces is reflected in the small numbers of *O. mülleri* which settle on the efferent vessel itself. Settlement on this vessel is restricted to the extreme tip and base of the gill, the areas not successfully cleaned by the epipodites. Judging by the high level of barnacle settlement another part of the platelets perhaps not effectively cleaned is that between the efferent vessel and knob e.

When only a few barnacles were found in a crab they were always settled on the gills. However when a high infestation was found the barnacles were also settled on the wall of the branchial chamber, cleaning appendages and even on the outside of the crab on the basal parts of the maxillipeds. *O. mülleri* was also

FIGURE 3. An excised gill of *C. sapidus* showing a large number of *O. mülleri* on the efferent side. The barnacles range from mature individuals (mat.) to small recently settled individuals (r.s.); ev, efferent vessel.

FIGURE 4. The tips of some setae from the epipodite of the third maxilliped of *C. sapidus*, showing the back-curved hooks (arrows).

FIGURE 5. Transverse sections through the peduncles of (a) *Lepas antifer*a and (b) *Octolasmis mülleri*. In *Lepas* the outer cuticle (cut.) is thick and underlying longitudinal muscles extensive (1 m.); cement cells (c.) are also present in the section. In *Octolasmis* the outer cuticle is much thinner (cut.) and the longitudinal muscles are reduced to a single band (1 m.); cement cells (c.) are also present as is part of the ovary (ov.)

occasionally found settled either on the peduncle or capitulum of other settled individuals under severely crowded conditions.

The movements and behavior of the cyprids in the branchial chambers prior to settlement are not known, but since some site selection occurs active searching probably takes place. Such behavior is common in cirripedes at settlement (see Crisp, 1974).

Although the majority of barnacles are found on the efferent side of the gills of blue crabs some barnacles were found on the afferent side and had presumably been taken into the hyperbranchial side of the branchial chamber as cyprids during the reversal of respiratory current by the crab. This reversal of respiratory current helps cleanse the branchial chamber of debris which has accumulated during the normal respiratory flow. It is possible that as the barnacle population on the efferent side of the gills increases, the cleaning appendages are unable to work effectively and debris accumulates. The host, therefore, reverses the respiratory current more frequently in order to remove the accumulated debris and in doing this takes more cyprids into the hyperbranchial side of the branchial chamber. It was interesting to find that all *O. mülleri* were settled on the afferent side of the gills in the branchial chambers of the crab *Ovalipes ocellatus*. The habits of *O. ocellatus* are different from those of *C. sapidus* in that it spends a larger proportion of time buried in sand. The normal respiratory flow of *O. ocellatus* is equivalent to the reversed respiratory flow of *C. sapidus* (see Pearse, Humm and Wharton, 1942).

Cyprids finally cement themselves to the gills a little way in from the margin of the platelets, both antennules being cemented to the same platelet by secretion from the cement glands within the cypris body (see Walker, 1971). There is apparently no preference shown by the cyprids for the upper or lower side of the platelets at settlement. Following permanent attachment the antennules are flexed thus drawing the body of the cyprid down onto the edges of the platelets. Metamorphosis then follows and the young adult *O. mülleri* emerges. The adult cement apparatus develops (see Walker, 1973) and as the young barnacle grows "adult" cement is laid down. This will initially fill between the two platelets where the cyprid settled, but later as more cement is produced it flows over and between neighboring platelets.

The adult stalk and cement apparatus of the sheltered *O. mülleri* can be compared with that of the related exposed lepad, *Lepas anatifera* (Lacombe and Liguori, 1969). Differences in structure are revealed in traverse sections of the peduncles of these two barnacles (Fig. 5a, 5b). The peduncular cuticle of *O. mülleri* is much thinner than that of *L. anatifera* and the underlying musculature is also much reduced. In *L. anatifera* all the cement cells are aggregated close to the capitulum-peduncle junction and are interconnected by secondary cement ducts. These secondary ducts, which are not lined with chitin, join together eventually forming the two primary ducts (chitin lined), which lead down the peduncle and open out at the ends of the antennules. In *O. mülleri* the cement cells are found throughout the length of the peduncle [c.f. *Pollicipes* (Kochler, 1889)], although the majority of the cells are found in the upper peduncular region. The two primary ducts extend up the peduncle for about two-thirds of its length

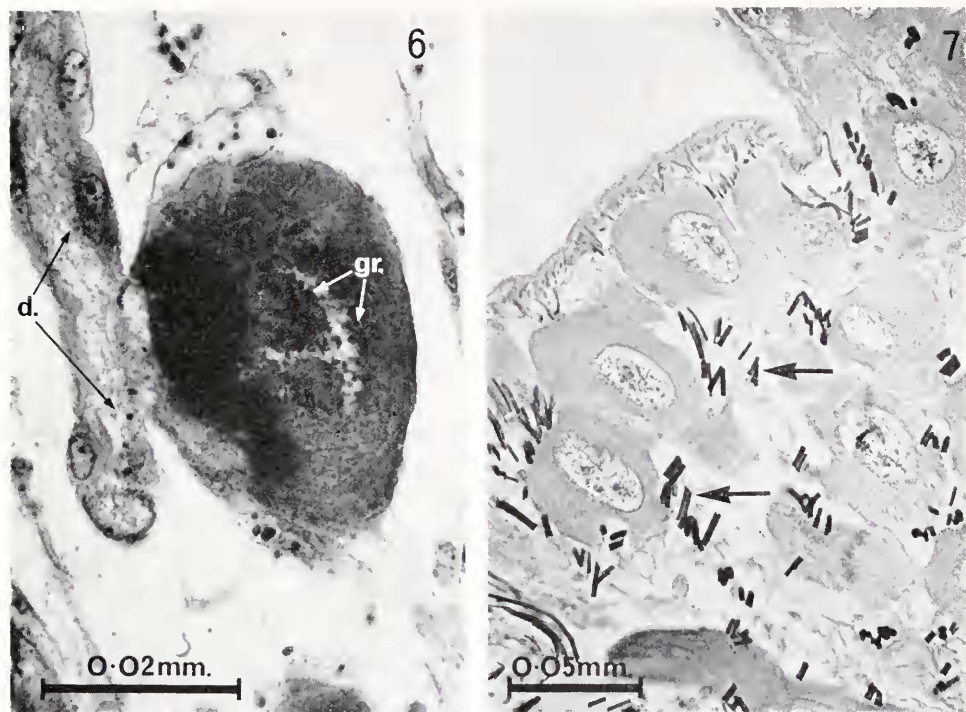


FIGURE 6. A cement cell of *O. mülleri* showing the connection with a collecting duct (d.) The dark mass is secretion which is aggregated around an intracellular canal; gr., granules; Azan.

FIGURE 7. Oblique muscles (arrows) between the cement cells of *Lepas anatifera*; Diazo-coupling for tyrosine.

and lead into the secondary ducts which connect with the cells (collecting ducts).

The cement cells of *O. mülleri* are about 50μ in diameter in an animal possessing a peduncle 2 mm long. Each cell contains a highly lobulated nucleus with a single nucleolus. There is an intracellular canal within each cell and this leads into the collecting duct. The secretion within the cell is aggregated close to the intracellular canal (Fig. 6); histochemical tests on this secretion confirm those of an earlier study on barnacle cement (Walker, 1970) which show it to be proteinaceous. Also in the cytoplasm there are distinct granules, 1μ in diameter, which stain intensely red with azan. Similar granules have been found in the cement cells of *Chelonibia testudinaria*, the turtle barnacle, and are thought to be lipofuscin granules (Walker, unpublished). There are in some cement cells of *O. mülleri* clear vacuoles, up to 5μ in diameter. The cement cells of *L. anatifera* are rounded in shape, $56\text{--}112 \mu$ in diameter (in a barnacle with a peduncle length of 4 mm), with spherical nuclei each containing 8–10 nucleoli. There is an extensive intracellular canal within each cell and this leads into a collecting duct. The region of the cytoplasm surrounding the intracellular canal is filled with secretion which as for *O. mülleri* reacts positively for proteins. Between the

cement cells of *L. anatifera* there are many oblique muscle fibers (Fig. 7), which may aid the extrusion of secretion from the cells (see Lacombe, 1970).

DISCUSSION

O. mülleri has been found on crabs which live in high salinity water, the crabs being either true oceanic crabs or spending part of their life cycle in the ocean. Pearse (1936), however, found an exception to this in *Uca minax* a crab which inhabits low salinity marshes. In the case of *C. sapidus*, the most common host of *O. mülleri* in Beaufort Inlet, the larval stages are spent in the ocean. As young crabs they migrate into low salinity water of estuaries, where they reach maturity after 1 year. Blue crabs mate in low salinity water, the mating taking place when the female is moulting for the final time (Judy and Dudley, 1970). The mated females then migrate back to high salinity water, where they spawn and where the larvae are released. Most males remain in the low salinity areas, only a few migrating back to the ocean with the females (Judy and Dudley, 1970). After the first spawn and hatch the females may re-enter the mouth of the estuary and spawn again, returning to the ocean for the second hatch. Finally, after spawning perhaps for a third time the females are thought to die in the ocean. Blue crabs rarely survive longer than 1 year after reaching maturity (Tagatz, 1968).

In trawls taken at Core Creek, in the Newport River upstream of the Beaufort Inlet where the salinity is 30‰ near the river bed only a single barnacle infested crab was taken, while at Adams Creek where the salinity close to the river bed was 16‰, *O. mülleri* was absent from all the blue crabs caught. These preliminary field observations help confirm Scarff's (1966) observations in the laboratory of the salinity tolerance of adult *O. mülleri*. She found that in water of salinity 20–40‰ the barnacles, which were left attached to pieces of excised gill, had open valves with the cirri extended. At 15‰ the valves were closed, but when the barnacles were returned to high salinity water 80% recovered after 24 hrs. At 10‰ valves were tightly closed and only 35% recovered after 24 hrs. At 5‰ the valves were tightly closed and none recovered. Salinity, therefore, appears to be a major factor limiting the distribution of *O. mülleri*.

DeTurk (1940) believed that the occurrence of *O. mülleri* was associated with the accumulation of debris in the branchial chambers of crabs, older blue crabs with large amounts of sand and other debris harboring the largest number of barnacles. He compared the infestation of dirty-gilled crabs, *L. emarginata*, *L. dubia* and *C. sapidus* with clean-gilled crabs, *O. ocellatus*, *P. spinimanus* and *C. ornatus* (see Table II), where few *O. mülleri* occur. *O. mülleri* settles on most crabs close inshore (Pilsbry, 1907) and therefore it is said to be a shallow water species (DeTurk, 1940; see Newman, 1967). Settlement is not host-specific and will take place on crabs of all age groups and sizes. However since juvenile crabs moult regularly, extruding the settled barnacles with the moult, the chance of observing *O. mülleri* on juvenile crabs is much less than on mature crabs. Although *O. mülleri* was found on many different crabs in Beaufort Inlet, *C. sapidus* is the most important host because it is the most common crab in this area (Judy and Dudley, 1971).

The respiratory current of the spiny lobster, *Puerulus seawelli*, was shown by Dinamani (1964) to affect the orientation of the cyprids of *Octolasmis stella* during initial settlement. They settled in such a position that following metamorphosis the young barnacle's cirral net was facing into the current. Specimens of *O. mülleri* were also found to be orientated to the respiratory current of the blue crab. Dinamani (1964) further explored the variation in certain features of the capitular valves of *O. stella*; he noted that the barnacles close to the outside of the branchial chambers of the lobster had armoured valves, whilst those barnacles better protected further in the branchial chamber had thinner, more delicate valves. Such differences due to situation were sought but not detected in *O. mülleri*.

In the relationship between the host crab and the epizoid barnacle most advantages lie with the barnacle. Once established in a branchial chamber it is protected, such protection allowing the reduction of capitular shell peduncular cuticle and musculature (cf. *Lepas anatifera*). A further advantage of being positioned in a branchial chamber is that there is a constant food supply brought in as suspended material in the crab's respiratory current. The presence of barnacles on the gills probably does not have any detrimental effects on the crab. However, bryozoans and nemerteans are regularly associated with barnacle infestations and all these epizoites would contribute greatly to the accumulation of debris on the gills and would consequently decrease the efficiency of the respiratory processes by impairing gill movements, reducing the amount of exposed gill surface and removing oxygen for their own needs.

The crabs main protection is ecdysis. After breeding the female blue crab has fulfilled her role in propagating the species and survival becomes less important. Moulting is terminated and she gradually becomes debilitated under epizoite attack.

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SUMMARY

1. *O. mülleri* was present on the gills of most crab species in Beaufort Inlet but not on *C. sapidus* further upriver indicating that salinity is probably a factor controlling the incidence of the barnacle.

2. The distribution of the barnacle on the individual gills of *C. sapidus* has been analyzed and the factors affecting this distribution discussed. The main factors are the cleaning action of the epipodites and the respiratory flow of the crab.

3. The barnacle settlement stage larva (cyprid) attaches to blue crab gills a short distance in from the gill margin. The orientation of the larva at settlement

is a response to the respiratory flow of the crab resulting in the cirral net of the young barnacle facing into the current.

4. The cement apparatus and internal stalk structures of *O. mülleri* and *Lepas anatifera* are compared.

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